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Agents for Biological Control of Purple Nutsedge, Cyperus rotundus L.

The Genus Bactra Stephens (Lepidoptera: Tortricidae: Olethreutinae) as a Major Source With Emphasis on the Biology and Potential Use of Bactra verutana Zeller

Abstract

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This publication surveys insects known to attack purple nutsedge, a worldwide noxious weed; summarizes studies done on host-plant specificity; discusses broadly the genus *Bactra* as a major source of insects that limit their attack to purple nutsedge; and focuses on *Bactra verutana* Zeller as a promising candidate for augmentation releases. The publication details studies done with *B. verutana* to determine its distribution, its host plants with and without stress, its biology, and ways to increase its effectiveness as a pest control agent.

Keywords: *Athesapeuta cyperi, Bactra* spp., *Bactra verutana,* chufa, *Cyperus esculentus, Cyperus rotundus,* integrated pest management, pest control (biological), purple nutsedge, weed control, weeds, yellow nutsedge

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The Genus *Bactra* Stephens (Lepidoptera: Tortricidae: Olethreutinae) as a Major Source, With Emphasis on the Biology and Potential Use of *Bactra verutana* Zeller

By Kenneth E. Frick

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Contents

Introduction

Among the more widespread weeds in the world are two perennial herbs that propagate primarily by means of underground tubers. These plants are in the sedge family, Cyperaceae, and are purple nutsedge, *Cyperus rotundus* L., and yellow nutsedge, *C. esculentus* L. Because these weeds are difficult to control, Holm et al. (1977) rated purple nutsedge as the world's worst weed and yellow nutsedge as the 16th worst.

Although purple nutsedge is considered to be nothing more than a weed (Holm et al. 1977), yellow nutsedge, in addition to being regarded as a weed, is also known for its beneficial qualities (Mulligan and Junkins 1976). The seeds and tubers of yellow nutsedge are listed as food for wildlife, primarily wildfowl (McAtee 1939, Martin and Uhler 1939, Martin et al. 1951). The tubers, called chufas, are grown for swine (Killinger and Stokes 1946, Poinar 1964a) or human consumption (Power and Chestnut 1923, Mulligan and Junkins 1976). Chufa has considerable potential as an oil crop in Canada. Yellow nutsedge is a good oil crop in southern China (Wang 1978). In fact, *C. esculentus* as a crop has been of sufficient importance that recommendations for control of some major pests have been made. For example, Satterthwait (1942), after discussing nine weevil species that attack yellow nutsedge in the Mississippi Valley, provided recommendations for their control. None of the weevils fed on the tubers. In southern China, a program was developed to control the primary insect pest of yellow nutsedge, *Bactra minima minima* Meyrick (As *B. phaeopis* Meyrick).

Because purple and yellow nutsedges are so difficult to control by any known means, biological control was resorted to at a relatively early date. In fact, the attempt in Hawaii to control purple nutsedge with insects appears to be the third oldest biological weed control project on record, being preceded only by the prickly pears, *Opuntia* spp., and lantana, *Lantana camara* L. (Goeden 1978).

In 1920–21, Williams (1922) made a preliminary survey for insects attacking purple nutsedge in the Philippines. He found a mealybug, a weevil, and the larvae of two borers: the moth *Bactra venosana* (Zeller) and the weevil *Athesapeuta cyperi* Marshall. These were used for host-plant specificity tests. When both proved to be sufficiently host-plant specific, they were released in 1925 (Pemberton 1948). Since that time, both species have been considered to be ineffective in the control of purple nutsedge in Hawaii (Andres and Davis 1973). In addition, both insects attack *C. esculentus* (Poinar 1964b; Habib 1976a, 1976b).

Despite this early failure to achieve adequate control of purple nutsedge, the search for insects feeding on it has continued. Concerted efforts to search for natural enemies have been made in India, with 21 species reported (Fletcher 1920, Sankaran and Srinath 1966, Tripathi 1969, Sankaran and Rao 1972); Pakistan, with 28 (Habib 1977); and the United States, with 39 (Satterthwait 1931; Vaurie 1951; Poinar 1964a, 1964b; Frick 1978). In the United States, particular attention has been given to the insects found on *C. rotundus* in Hawaii, southern California, and Mississippi (table 1).

Unfortunately, probably at least 50% of those species have too broad a host range to be considered as biological control agents. Because of this, Habib (1977) prepared a worldwide list of stenophagous insects—that is, those having a known host-plant spectrum sufficiently restricted that they could be considered as candidates for further study. There are 30 species, all from *Cyperus* spp.

Of those 30 species, 8 or 27% are in the genus *Bactra*. Thus, in this list, as in other lists from various faunas, species of *Bactra* constitute an important segment of the potentially stenophagous insect species that can be considered as useful biological control agents. In fact, wherever the biological control of purple or yellow nutsedge is under study, *Bactra* spp. are among the first of the insects to be considered. Such has been the case in Spain (Garcia-Baudin et al. 1979); Pakistan (Habib 1976a); India (Sankaran and Srinath 1966); Australia (Cashmore and Campbell 1946); Ecuador (Cevallos and Navia 1971); and the United States, in Hawaii (Poinar 1964b), California (Poinar 1964a, Keeley et al. 1970), and Mississippi (Frick 1978). The U.S. species are included in table 2. Similarly, Pecora (1977), considering the possibility of implementing the biological control of purple nutsedge in Italy, suggested the introduction of *Bactra verutana*.

However, *Athesapeuta cyperi* should not be overlooked as a useful biological control agent. It and five *Bactra* species are the only species of insects in purple nutsedge that have been studied in detail. *A. cyperi* is quite host-plant specific, being confined to *C. rotundus, C. esculentus,* and a few related species of

Cyperus (Poinar 1964b, Habib 1976b). It is potentially more damaging to its host plants than are species of *Bactra*. *A. cyperi* larvae attack the basal bulbs, killing them (Habib 1976b). In contrast, Habib (1976a) reported that 28% of the basal bulbs of purple nutsedge plants attacked by a single larva of *B. venosana* resprouted. In the case of *B. minima minima,* 35% resprouted. Frick et al. (1979), working with *B. verutana,* noted that 83% of the basal bulbs of attacked purple nutsedge plants and 71% of the basal bulbs of yellow nutsedge resprouted. Thus, in spite of its lower reproductive potential and longer life cycle, *A. cyperi* can cause noticeable damage in nature. Habib (1976b) reported a field infestation as high as 16% in Pakistan, while, in India, infestations of 16.5% and 20% of the plants have been reported (Sankaran and Srinath 1966).

Table 1—*Arthropods reared from, or repeatedly associated with,* Cyperus rotundus *L. in the United States, including Hawaii*

Order	Family	Genus	Species	Distribution	Remarks	Sources
Acari	Tetranychidae	*Tetranychus*	*urticae* Koch	Mississippi	Two-spotted spider mite; in greenhouse, not common	Determined by R. E. Furr, USDA, ARS (ret.)
Thysanoptera	Thripidae	*Dorcadothrips*	*coespitis* Preisner	Southern California		Poinar 1964a
		Frankliniella	*fusca* (Hinds)	Mississippi	Tobacco thrips; scarce	Frick 1978
		Taeniothrips	*cyperaceae* Bianchi	Hawaii	Also attacks *C. esculentus*	Poinar 1964b
	Phlaeothripidae	*Haplothrips*	*sakimurai* Moulton	Hawaii		Poinar 1964b
Homoptera	Aleyrodidae	*Aleurocybotus*	*occiduus* Russell	Southern California	Also attacks *C. esculentus*	Poinar 1964a, 1965
	Aphididae	*Rhopalosiphum*	*rufiabdominalis* (Sasaki)	Hawaii, Mississippi	Rice root aphid; also attacks *C. esculentus*	Beisler 1977, Frick 1978, Poiner 1964b
		Schizaphis	*cyperi* (van der Goot)	Hawaii		Poinar 1964b
	Cicadellidae	*Deltocephalus*	*sonorus* Ball	Mississippi		Frick 1978
		Draculacephala	*portola* Ball	Mississippi		Frick 1978
		Exitianus	*exitiosus* (Uhler)	Mississippi	Gray lawn leafhopper	Frick 1978
		Graminella	*nigrifrons* (Forbes)	Mississippi	Blackfaced leafhopper; also attacks *C. esculentus*	Beisler 1977, Frick 1978
		Macrosteles	*fascifrons* (Stal)	Mississippi	Aster leafhopper	Frick 1978
		Paraphlepsius	*abruptus* (DeLong)	Mississippi		Frick 1978
	Coccidae	*Saissetia*	*nigra* (Nietner)	Hawaii		Poinar 1964b
	Delphacidae	*Delphacodes*	*puella* (Van Duzee)	Mississippi		Frick 1978
	Pseudococcidae	*Dysmiococcus*	*brevipes* (Cockerell)	Hawaii, southern U.S.	Also attacks *C. esculentus*	McKenzie 1967, Poinar 1964b
		Geoccoccus	*radicum* Green	Hawaii		Poinar 1964b

Table 1—*Arthropods reared from, or repeatedly associated with,* Cyperus rotundus *L. in the United States, including Hawaii—Continued*

Order	Family	Genus	Species	Distribution	Remarks	Sources
		Phenacoccus	*solani* Ferris	Southern one-half of U.S.	Common in greenhouse at Stoneville, Miss.; also attacks *C. esculentus*	McKenzie 1967; Poinar 1964a; determined by D. R. Miller, Systematic Entomol. Lab., USDA, ARS, Beltsville, Md.
		Rhizoecus	*cacticans* (Hambleton)	California		McKenzie 1967, Poinar 1964a
Coleoptera	Chrysomelidae	*Chaetocnema*	*pulicaria* Melsheimer	Mississippi	Corn flea beetle; also attacks *C. esculentus*	Beisler et al. 1977, Frick 1978
	Curculionidae	*Anacentrinus*	*blanditus* (Casey)	Mississippi		Frick 1978
		Athesapeuta	*cyperi* Marshall	Hawaii (introduced)	Introduced from the Philippines in 1925; also attacks *C. esculentus*	Poinar 1964b, Williams 1931
		Lissorhopterus	*oxyzophilus* Kuschel	Mississippi	Rice water weevil; adult feeding only; also associated with *C. esculentus*	Determined by D. R. Whitehead, Systematic Entomol. Lab., USDA, ARS, Beltsville, Md.
		Sphenophorus	*callosus* (Olivier)	Eastern U.S.	Southern corn billbug; also attacks *C. esculentus*	Frick 1978, Satterthwait, 1931, Vaurie 1951
			cariosus (Olivier)	Hawaii, eastern U.S.	Nutgrass billbug; also attacks *C. esculentus*	Frick 1978, Poinar 1964b, Satterthwait 1931, Vaurie 1951
			cubensis Buchanan	Florida, Caribbean region		Vaurie 1951
			phoeniciensis (Chittenden)	California, Arizona		Poinar 1964a, Satterthwait 1931, Vaurie 1951
			venatus vestitus (Chittenden)	Southeastern U.S.	Hunting billbug; also attacks *C. esculentus*	Frick 1978, Vaurie 1951

Table 1—*Arthropods reared from, or repeatedly associated with,* Cyperus rotundus *L. in the United States, including Hawaii—Continued*

Order	Family	Genus	Species	Distribution	Remarks	Sources
Lepidoptera	Ctenuchidae	*Cisseps*	*fulvicollis* (Hübner)	Mississippi		Frick 1978
	Glyphipterygidae	*Glyphipterix*	*impigritella* (Clemens)	Mississippi, Virginia	Also attacks *C. esculentus*	Beisler 1977, Frick 1978
	Hesperidae	*Atalopodes*	*campestris* (Boisduval)	Mississippi	In greenhouse at Stoneville, rare	Determined by J.M. Burns, U.S. National Museum of Natural History, Washington, D.C.
		Lerema	*accius* (Smith)	Mississippi	In greenhouse at Stoneville, rare	Frick 1978
	Noctuidae	*Pseudaletia*	*unipuncta* (Haworth)	Hawaii; widespread in the U.S.	Armyworm; usually feeds on grasses and cereal crops	Crumb 1956, Frick 1978, Poinar 1964b
		Spodoptera	*exempta* (Walker)	Hawaii	Nutgrass armyworm	Poinar 1964b
			frugiperda (J. E. Smith)	Widespread in the U.S.	Fall armyworm, usually feeds on cereals and other grasses	Frick 1978
			mauritia Boisduval	Hawaii	Lawn armyworm	Poinar 1964b
			ornithogalli (Guenée)	Primarily in southeastern U.S.	Yellow-striped armyworm, a very general feeder	Frick 1978
	Pyralidae	*Elasmopalpus*	*lignosellus* (Zeller)	Southern U.S.	Lesser cornstalk borer	Frick 1978

Source: based on table 1 in Frick (1978)

Table 2—*Worldwide list of the species in the genus* Bactra *known to feed on species of plants in the family Cyperaceae*

Subgenus	Species and synonym	Distribution	Host plants reported in nature						Sources
			Cyperaceae			Juncaceae	Typhaceae	Graminae	
			Cyperus		Other genera				
			rotundus and/or *esculentus*	Other species		*Jencus* species	*Typha* species		
Bactra	Stephens, 1834;								
	bactrana Kennel, 1901 (*graminivora* Meyrick, 1922)	Southern Europe, Asia, Africa	*rotundus* L.						Diakonoff 1959, 1963, 1973; Fletcher 1932; Habib 1976a, 1977
	clarkei Diakonoff, 1964	Guyana		Species not named					Diakonoff 1964
	furfurana (Haworth, 1811)	North America, Europe, North Africa, Asia	Both species plus *esculentus* var. *sativus* Boeck		*Scirpus* sp.	Species not named			Diakonoff 1959, 1964; Forbes 1923; Heinrich 1926; Garcia-Baudin 1979
	honesta Meyrick 1909	India, Japan		*serotinus* Rottb.		*effusus* L.			Diakonoff 1959, 1964; Shibata 1971
	lanceolana (Hubner, 1796)	North America, Europe, North Africa, Asia	Both species plus *esculentus* var. *sativus* Boeck			Species not named			Diakonoff 1959, 1963; Garcia-Baudin 1979; Habib 1977; Heinrich 1926
	robustana (Christoph, 1872)	Europe, North Africa, Asia		*Scirpus maritimus* L.					Diakonoff 1956, 1959, 1964
Chiloides	Butler, 1881;								
	copidotis Meyrick, 1909 (*commensalis* Meyrick 1922)	India, Sri Lanka	*rotundus* L.						Diakonoff 1964, Fletcher 1932, Habib 1977
	philocherda Diakonoff, 1964	U.S. (Florida) American Tropics, Africa		Species not named					Diakonoff 1964
	simpliciana Chretien, 1915	North Africa, Middle East		*conglomeratus* Rottb.					Diakonoff 1959, 1963, 1964
	straminea (Butler, 1881)	Hawaii			"Sedges" (*Carex* spp.?)				Diakonoff 1956, 1959; Williams 1931
	venosana (Zeller, 1874) (*truculenta* Meyrick, 1909)	Southern Europe, North Africa, Asia, Australia, South Pacific, Hawaii	Both species	*brevifolius* (Rottb.) *bulbosus* Vahl, *difformis* L., *eleusinoides* Kunth, *iria* L., *tenuifolius* (Steud.)					Diakonoff 1956, 1959, 1964, 1967; Ghosh 1922; Habib 1976a, 1977; Poinar 1964b.

Table 2—*Worldwide list of the species in the genus* Bactra *known to feed on species of plants in the family Cyperaceae — Continued*

Subgenus	Species and synonym	Distribution	Host plants reported in nature						Sources
			Cyperaceae			Juncaceae	Typhaceae	Graminae	
			Cyperus		Other genera				
			rotundus and/or *esculentus*	Other species		*Jencus* species	*Typha* species		
Nannobactra	Diakonoff, 1956;								
	blepharopis Meyrick, 1911	Australia	*rotundus* L.						I. F. B. Common (personal communication)
	cultellana Zeller, 1877	U.S. (Florida), Colombia, Paraguay	*esculentus* L.						Diakonoff 1964
	maiorina Heinrich, 1923	U.S.	"Grass" (=nut-grass or nutsedge, *Cyperus esculentus?*)		*Scirpus fluviatalis* (Torr.)		*latifolia* L.		Diakonoff 1964; Forbes 1923; Heinrich 1926
	minima minima Meyrick, 1909 (*phaeopis* Meyrick, 1911)	Southeast Asia, South Pacific	Both species						Diakonoff 1956, 1959, 1964; Habib 1976a, 1977; Sankaran and Srinath 1966; Wang 1978
	oceani Diakonoff, 1956	Fiji	*rotundus* L.						Diakonoff 1956, M. K. Kamath (personal communication), Habib 1977
	verutana Zeller, 1875; subsp. *chrysea* Heinrich, 1926, (*dasioma* Diakonoff, 1963)	Southern U.S., Mexico (Baja California Norte), Caribbean region, Panama, Paraguay, South Africa	Both species	*iria* L. *papyrus* L.	*Scirpus* spp.	Species not named		*Panicum dichotomiflorum* Michx.	Beisler 1977, Diakonoff 1964, Forbes 1923, Frick and Garcia 1975, Heinrich 1926, Jefferson and Humphrey 1964
Unknown	Unnamed sp.	Colombia	*rotundus* L.						Altieri and Doll 1978
	Unnamed sp.	Ecuador	*rotundus* L.						Cevallos and Navia 1971

Source: based on table 2 in Frick (1978).

The Genus *Bactra* Stephens, 1834, As a Source of Biocontrol Agents

The prominence of *Bactra* spp. is due not only to their apparently restricted host-plant range and to the obvious damage inflicted on their host plants, but also to their wide distribution. For example, Diakonoff (1956, 1959, 1963, 1964) listed 87 species, of which the host plants were known for 16, or 18%. Since that time, the host plant of an Australian species, *B. blepharopis* Meyrick, has been determined (Frick 1978). These 17 species are distributed in every continent and on many islands where warm-to-temperate climates prevail (table 2).

The genus *Bactra* has been divided into five subgenera by Diakonoff (1956, 1963). Of the 17 named species for which host plants are known, 6 are in *Bactra,* 5 in *Chiloides,* and 6 in *Nannobactra* (table 2). There is a noticeable overlapping of the geographic ranges of these three subgenera. This is illustrated in the distributions of the species for which host plants are known. Each of the two remaining subgenera is monotypic, and the host plants of these two species remain unknown. One, *Noterula* Meyrick, 1892, is based on a single species in New Zealand. The other, *Spinobactra* Diakonoff, 1963, was erected for a single species found in southern Africa.

Recorded Host Plants

The larvae of *Bactra* spp. feed primarily on plants in the sedge family Cyperaceae. In fact, each of the 17 named species listed in table 2 has been reported from one or more of the sedges. The genus *Cyperus* predominates as host, with 14 species of *Bactra* recorded on *Cyperus* species; 9 of these *Bactra* spp. are specifically from *C. rotundus*. By comparison, only four species of *Bactra* are reported from species of *Juncus,* one on *Typha,* and there is a single record from a grass. However, it should be remembered that these rearing records represent only 17 of 88 species of *Bactra*. Thus, it is obvious that much more collecting and rearing need to be done before the definitive host range of the genus *Bactra* is known. The two unnamed species from Colombia and Ecuador reared from *C. rotundus* are not included in these totals because either or both may belong to any of the four named species reported from South America: *B. clarkei, B. cultellana, B. philocherda,* and *B. verutana* (table 2).

Experimental Host-Plant Spectrum

Studies on the acceptance of various plants by the larvae have been conducted with only three species of *Bactra* (table 3). Two of them, *B. minima minima* and *B. venosana,* were tested in Pakistan by Ghani (1975) and Habib (1976a). In addition, Poinar (1964b) studied the host-plant range of the Hawaiian population of *B. venosana,* which originated in the Philippines. Similarly, with co-workers, I tested the population of *B. verutana* found at Stoneville, Miss.

Within the family Cyperaceae, the larvae were confined to the genus *Cyperus* with the exception of small percentages developing on two species of *Fimbristylis* in Pakistan. High percentages of development of the two Asian species occurred only on *C. eleusinoides* and *C. esculentus*. In contrast, I found that six species of *Cyperus,* other than *C. esculentus* and its var. *sativus,* were heavily attacked (table 3). Thus *B. verutana* appears to have the broadest host-plant range of any known species of *Bactra*. It has fed heavily on eight species of *Cyperus* in Mississippi as well as being considered a pest of *C. papyrus* in southern California (Jefferson and Humphrey 1964).

Experimentally, there is only a single instance of a grass being even a semisatisfactory host plant (Ghani 1975). Only 1 of 15 third-instar larvae of *B. venosana* completed development, and that one required about twice as long to develop (45 vs. 21 days) as larvae exposed to *C. rotundus* (table 3). Of the dicotyledonous plants tested, only on 2-week-old turnip plants was there feeding sufficient for pupation of 10-day-old (third-instar) larvae of *B. verutana*. Only 18% pupated, and the pupae were small, producing moths two-thirds to three-fourths the size of moths reared on purple or yellow nutsedge.

Host-Plant Range and Conflicts of Desired Results

The total (definitive) host-plant spectrum has probably not been determined for any species of *Bactra*. However, the presently known host-plant ranges of *Bactra* spp. provide possible conflicts of desired results if efforts were made to introduce these biological control agents into specific geographical locations. For example, five of the host plants of *B. verutana* (*C. esculentus, C. erythrorhizos, C. iria, C. rotundus,* and *C.*

Table 3—*Results of tests for host plants of* Bactra minima minima *Meyrick in Pakistan,* B. venosana *(Zeller) in Pakistan and Hawaii, and* B. verutana *Zeller at Stoneville, Miss.*

Host plant	Development completed (%)						Sources			
	B. minima minima		*B. venosana*		*B. verutana*		Ghani 1975, Habib 1976a	Poinar 1964b	Frick 1975	K. E. Frick (unpublished data)
	1st instar	3d instar	1st instar	3d instar	1st instar	3d instar				
Cyperaceae										
Carex wahuensis C. A. Mayer var. *rubiginosa* R. Krauss			–					X		
Cyperus alternifolius L. (umbrella flatsedge)			+					X		
Cyperus compressus L.					+[1]					X
Cyperus difformis L. (small flower umbrella plant)	+(7)	+(13)	+(7)	+(33)			X			
Cyperus eleusinoides Kunth	+(53)	+(53)	+(40)	+(53)			X			
Cyperus engelmanni Steud.					+[1]					X
Cyperus erythrorhizos Muhl. (redroot flatsedge)					+[1]					X
Cyperus esculentus L. (yellow nutsedge)	+(53)	+(66)	+(73)		+(65)		X	X	X	X[2]
Cyperus esculentus var. *sativus* Boeck (chufa)					+					X
Cyperus globosus All.	–	+	–	+			X			
Cyperus iria L. (rice flatsedge)	+		+(7)	+(13)	+		X		X	
Cyperus odoratus L.					+[1]					X
Cyperus papyrus L. (papyrus)			+					X		
Cyperus strigosus L. (false nutsedge)					+[1]					X
Cyperus tenuifolius (Stend.) Dandy in Excell.					+[1]					X
Eleocharis obtusa (Willd.) Schultes (blunt spikerush)			–					X		
Fimbristylis dichotoma (L.) Vahl	–	+(13)	–	+			X			
Fimbristylis feruginea (L.) Vahl	–	+(7)	–	+(7)			X			
Fimbristylis polymorpha Boeck			–					X		
Scirpus lacustris L.			–					X		
Gramineae										
Avena sativa L. (oat)	–	–	–	–			X	X		
Bromus catharticus Vahl (rescue grass)			–					X		
Dactylis glomerata L. (orchard grass)			–					X		
Festuca elatior L. (meadow fescue)			–					X		
Horedum vulgare L. (barley)	–	–	–	–			X	X		

Table 3—*Results of tests for host plants of* Bactra minima minima *Meyrick in Pakistan,* B. venosana *(Zeller) in Pakistan and Hawaii, and* B. verutana *Zeller at Stoneville, Miss.—Continued*

Host plant	Development completed (%)						Sources			
	B. minima minima		*B. venosana*		*B. verutana*		Ghani 1975, Habib 1976a	Poinar 1964b	Frick 1975	K. E. Frick (unpublished data)
	1st instar	3d instar	1st instar	3d instar	1st instar	3d instar				
Lolium perenne L. (perennial ryegrass)			–					X		
Oryza sativa L. (rice)	–	–	–	–	–		X		X	
Panicum dichotomiflorum Michx. (fall panicum)					–					X
Pennisetum glaucum (L.) R. Br. (pearl millet)	–	–	–	–			X			
Poa annua L. (annual bluegrass)			–					X		
Sorghum halepense (L.) Pers. (johnsongrass)			–		–			X	X	
Sorghum sudanense (Piper) Stapf. (sudangrass)	–	–	–	+(7)[3]			X			
Triticum aestivum L. (wheat)	–	–	–	–			X	X		
Zea mays L. (maize)	–	–	–	–			X	X		
Juncaceae										
Juncus bufonius L. (toad rush)			–					X		
Luzula campestris (L.) DC. var. *hawaiiensis* (Buch.)			–					X		
Typhaceae										
Typha angustata Bory and Chaub. (cattail)	–	–	–	–			X			
Brassicae										
Brassica rapa L. (turnip)					–	+(18)				X
Leguminosae										
Pisum sativum L. (English pea)			–	–			X			
Malvaceae										
Gossypium hirsutum L. (cotton)					–					X
Umbelliferae										
Daucus carota L. var. *sativus* Hoffm. (carrot)	–	–	–	–			X			

[1]From southern Illinois. Identified by John Simmers, Waterways Experiment Station, Vicksburg, Miss., U.S. Army Corps of Engineers.

[2]Frick et al. (1979); percentage of survival on *C. rotundus* was 90%.

[3]Developmental time was 45 days vs. 21 days when *C. rotundus* was the host plant.

strigosus) are considered weeds (Holstun 1971). However, seeds of two of those species (*C. erythrorhizos,* and *C. strigosus*) are taken in small-to-moderate quantities by ducks (Martin and Uhler 1939), and seeds of three of them—common, widespread species (*C. compressus, C. erythrorhizos,* and *C. strigosus*)—are frequently eaten by a number of birds (Martin et al. 1951). The tubers of *C. esculentus, C. esculentus,* var. *sativus, C. rotundus* and *C. strigosus* are of special value to waterfowl (McAtee 1939). Martin et al. (1951) placed chufa (*C. esculentus*) as probably of greater value to wildlife than all other *Cyperus* spp. combined. Chufa is also grown as food for swine (Killinger and Stokes 1946) and for human consumption (Power and Chestnut 1923, Mulligan and Junkins 1976). Of the remaining *Cyperus* species, one (*C. papyrus*) is grown as an ornamental. In addition, *B. verutana* has been reported from species of *Scirpus, Juncus,* and *Panicum* (table 2); a number of species in all three genera have been reported as providing food for wildlife (Martin et al. 1951).

Before either of the Southeast Asian *Bactra* species (*B. minima minima* and *B. venosana*) are introduced, the host-plant spectrum of each species should be determined. For example, both species are known to attack *C. esculentus* (table 2). The most destructive pest on that crop is *B. minima minima* (as *B. phaeopis*), and measures for its control have been developed (Wang 1978). Although *B. minima minima* has been reared from only four species of *Cyperus, B. venosana* has been reared from 10, including *C. papyrus* (table 2 and 3). Also, third-instar larvae of both these insects were reared experimentally from two species of *Fimbristylis* (Habib 1976a). Likewise, McAtee (1939) reported that seeds of plants in *Fimbristylis* were fed on by ducks to some extent.

Habib (1977), in her discussion of the possibilities for the biological control of *C. rotundus,* also warns of potential conflicts of desired results elsewhere. She notes in particular the widespread use of *C. esculentus* as a vegetable or an oil crop in many parts of the world. Also important is her reference to Wilson (1960), who pointed out the forage value of *C. retzii* Nees and the erosion control value of *C. victoriensis* Clarke, both species native to Australia.

Thus, based on studies to date, species of *Bactra* should not be imported into other geographic areas until they have been thoroughly tested on the potential local host plants and the value of each of them has been determined for both man and wildlife.

Life History and Biology

Among the earliest reports of *Bactra* spp. attacking *C. rotundus* is that of Ghosh (1922), who worked with *B. venosana* in India. It was at about this time that the earliest exploration for insects on purple nutsedge began in the Philippines (Williams 1922), which resulted in the introduction of *B. venosana* into Hawaii in 1925 (Williams 1931). Later, Williams (1931) briefly described the biology and the effectiveness of that introduced insect.

Following that, little attention was given to the biocontrol of purple nutsedge for several decades. However, interest was renewed in the early 1960's and has continued. Poinar (1964a) began with observations of *B. verutana* in southern California in 1962–63. In 1963, he went to Hawaii for several months to study *B. venosana* (Poinar 1964b). At approximately the same time, Sankaran and Srinath (1966) were studying the biology of *B. minima minima* in India, while in Pakistan M. A. Ghani began a study of a species of *Bactra* tentatively identified as *bactrana* Kennel (Habib 1977). Ghani quickly distinguished three species—*B. bactrana, B. minima minima,* and *B. venosana*—on which he later reported (Ghani 1975). These studies were followed by the work of Keeley et al. (1970) on *B. verutana* found on *C. esculentus* in California. In Japan, Shibata (1971) studied *B. honesta* as an insect enemy of the perennial *C. serotinus* Rottb., a weed of rice fields. In Ecuador, Cevallos and Navia (1971) reported on the biology of an unnamed species of *Bactra* attacking *C. rotundus.* A comparison of the life histories of two species (*B. minima minima* and *B. venosana*) was made in Pakistan by Habib (1976a). Simultaneously, Frick and Garcia (1975) were studying the biology of *B. verutana* in Mississippi. Later, Wang (1978) determined the life history of *B. minima minima* (as *B. phaeopis*) in southern China, where the insect is considered a pest of *C. esculentus.* Most recently, Garcia-Baudin et al. (1979) worked with two species of *Bactra* (*B. furfurana* and *B. lanceolana*) in Spain, where they attack both *C. rotundus* and *C. esculentus.*

These studies and observations describe a similar life history for six named and one unnamed species of *Bactra.* In brief, the annual life history begins with the

coming of warm weather in temperate climates, or it is continuous in more tropical situations. For example, in Pakistan both *B. minima minima* and *B. venosana* breed year-round at Karachi but only from April to November at Rawalpindi, where both species overwinter as larvae (Habib 1976a). In the case of *B. verutana* in west-central Mississsippi, although both large larvae and pupae were present in the fascicles of the host as winter began, only the pupal stage survived (Frick and Garcia 1975).

A life cycle requires about 30 days, and the duration of each stage requires approximately the number of days shown as follows: preoviposition, 2; egg, 3; larval, 14–18; pupal, 6–7. The eggs are laid on the leaves, primarily on the upper surface (fig. 1), shingled, or overlapping each other, in rows generally in the midrib groove (Williams 1931, Poinar 1964b, Sankaran and Srinath 1966, Habib 1976a). The newly hatched larvae either feed on the upper surface of the leaves, particularly where they are appressed, resulting in skeletonizing, or they bore into the leaves, where their feeding forms mines (fig. 2). As they grow, the larvae congregate in the whorl, where they feed on the youngest foliage. When about one-half grown, they bore into the fascicle, usually one larva per plant, where they feed down to the basal bulb (fig. 3).

The number of larval instars has been determined for three species. Habib (1976a) found four in *B. venosana* and usually four but a few with five in *B. minima minima;* Frick and Wilson (1978) reported that 35% of *B. verutana* larvae reared on *C. rotundus* had four instars, 58% had five, and 7% had six instars. Developmental periods were observed for larvae and pupae combined, and developmental times lengthened as the number of the instars increased. Larvae of *B. minima minima* with four instars required an average of 22 (20–25) days, while 5-instar larvae required an average of 28 (27–29) days (Habib 1976a). Four-, 5-, and 6-instar larvae of *B. verutana* averaged 18 (15–21), 23 (18–27), and 30 (28–32) days, respectively, for larval and pupal development (Frick and Wilson 1978).

As the larvae approach maturity, they line their tunnels in the fascicle with a silken tube in which they pupate. Pupation generally occurs below the soil surface. Just before moth emergence, the mature pupa works its way up the fascicle and partially out of a prepared exit "window" above the soil surface.

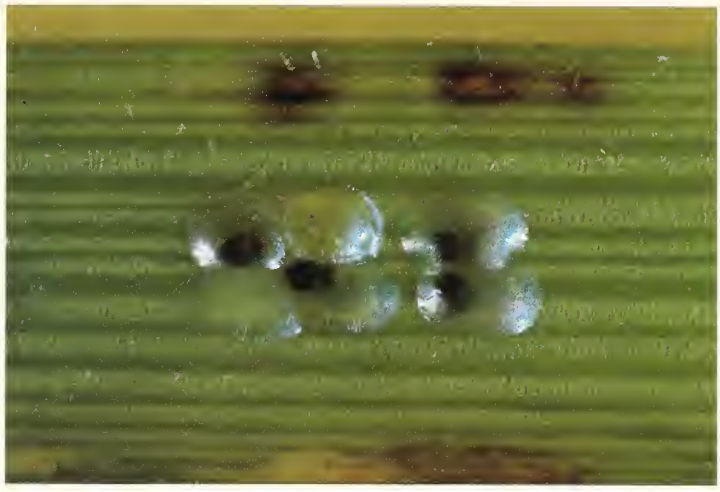

Figure 1.—Eggs of *B. verutana* laid on a leaf on *C. rotundus*.

Figure 2.—Neonate larva of *B. verutana* on a leaf of *C. rotundus* (top), together with eggs laid in the midrib groove (left) and a leaf mine made by the feeding of a neonate larva (right).

Figure 3.—Full-grown larva on *B. verutana* in the fascicle of *C. rotundus*.

Injury to Host Plants

The damage that the larvae do to the host plant has been described briefly for six named and one unnamed species of *Bactra* from six countries throughout the world as follows: *B. furfurana* and *B. lanceolana* in Spain (Garcia-Baudin et al. 1979); *B. minima minima* and *B. venosana* in Pakistan (Habib 1976a) and India (Ghosh 1922, Sankaran and Srinath 1966); *B. honesta* in Japan (Shibata 1971); *B. venosana* in Hawaii (Williams 1931, Poinar 1964b) and Mississippi (Frick and Garcia 1975); and a *Bactra* spp. in Ecuador (Cevallos and Navia 1971). The minor damage caused by the skeletonizing and mining of the small larvae feeding on the leaves for the first few days has generally been overlooked. These brief, general reports of injury are usually confined to a description of the withering and death of the innermost leaves, or deadhearting. That condition results from one-half to full-grown larvae feeding in the fascicle. In smaller plants, all the leaves may be killed; in larger ones, the visible injury may remain confined only to the central one to four leaves.

The larvae also feed to some extent on the basal bulb. The latter is usually not killed, but in response to injury, it may sprout one or more new shoots. The percentage of basal bulbs that resprouted following exposure to a single larva per shoot has been determined for three species of *Bactra*. In Pakistan, Habib (1976a) reported that 28% of the basal bulbs of purple nutsedge plants attacked by a larva of *B. venosana* resprouted; 35% attacked by *B. minima minima* resprouted. Frick et al. (1979), working with *B. verutana,* noted that 83% of the basal bulbs of attacked *C. rotundus* plants resprouted.

Habib (1976a) determined that a single larva of *B. minima minima* attacked an average 2.3 (range 1–4) plants of unspecified age during maturation, of which 33% sprouted new shoots. Thus, this species could kill 147 plants/100 larvae. However, *B. venosana* larvae attacked an average of only 1.8 (range 1–2) plants of unspecified age per larva, with 28% sprouting new shoots. Therefore, this species could kill 131 plants/larvae. Frick et al. (1979) infested plants 14–18 days old with *B. verutana* and found that a single larva attacked an average 1.6 (range 1–3) plants during development. However, 83% sprouted new shoots, so only 27 of these mature plants would be killed per 100 larvae.

No instance has been reported of a natural population of a *Bactra* species providing adequate control of *C. rotundus*. A number of reasons for this have been put forth over the years; these factors are as follows:

1. Poor synchronization in temperate climates—that is, early season growth of the host plants with late-season increase of moth populations. Frick and Garcia (1975) found that low winter temperatures reduced overwintering populations of *B. verutana* by 85%–90% in west-central Mississippi. They further showed that the numbers of moths increased slowly and that it was early August before damaging populations appeared. In central California, damaging populations were present by early July, 1 month earlier (Keeley et al. 1970).
2. Rarely more than one larva per plant, even though numerous eggs may be deposited on the leaves of that plant (Poinar 1964a, Sankaran and Srinath 1966). Frick and Garcia (1975) showed in three tests that 22%, 50%, and 90% of basal bulbs resprouted following feeding by one larva of *B. verutana* per plant; resprouting from the feeding of two larvae per plant was: 0%, 29%, and 60%; following the feeding of five larvae per plant it was: 0%, 31%, and 10%.
3. Larvae not feeding on the tubers and with limited feeding on the basal bulb, resulting in a relatively high percentage of basal bulb survival with continued production of new aerial shoots and tubers (Williams 1931, Sankaran and Srinath 1966, Keeley et al. 1970, Frick and Garcia 1975, Habib 1976a). Frick and Garcia (1975) showed that resprouting from plants fed on by one larva each amounted to 22%, 50%, and 90% in three tests; Habib (1976a) reported 35% resprouting following feeding by *B. minima minima* and 28% by *B. venosana*.
4. Parasitism (Williams 1931; Andres and Davis 1973; Poinar 1964a, 1964b). Although parasites are mentioned by nearly all the authors, only in Hawaii and southern California (Poinar 1964a) are they considered to be a limiting factor.

With one or a combination of these deterrents contributing to the lack of reported economic control by a native species of *Bactra* anywhere in the world, other approaches to the biological control of *C. rotundus* are called for.

Alternative Methods for Biocontrol of Purple Nutsedge

Two methods are available, and both have been considered and tried to a limited extent. The first is the classical approach, involving the introductions of exotic host-plant-specific species. The other consists of augmenting the natural populations of native species with any technique that will increase their numbers.

Introductions of Exotic Host-Plant-Specific Species

The classical approach to the biological control of *C. rotundus* began in 1925 with the introduction into Hawaii of two insects from the Philippines: *B. venosana* and *Athesapeuta cyperi*. Considered either individually or in combination, they have not provided satisfactory control (Williams 1931, Poinar 1964b, Andres and Davis 1973). Both species were introduced into Fiji in 1932, again with unsatisfactory results (Parham 1940, Frick 1978). These two species were brought to Australia for study from 1937 to 1940. Neither was released, both because of their failure in Hawaii and because of the probability that they would attack desirable native sedges. Recent releases of these two species plus *B. minima minima* have been made in Barbados, Cook Islands, and Tonga (Habib 1977). These introductions are too recent to have been evaluated.

In 1978, I doubted the value of introducing exotic insect species into any locality having ecological homologues—that is, where native species of *Bactra* already occur or where there are indigenous weevils whose larvae bore into *C. rotundus* and feed on the basal bulb. For example, in the southeastern United States, there are three species of *Bactra* known from *C. rotundus* (table 1). But where there are unfilled ecological niches, introductions are appropriate and combinations of species appear to be better than a single species. For example, *A. cyperi* has been included in previous introductions with *B. venosana*. It attacks from 16% to 20% of the plants in Pakistan and India (Sankaran and Srinath 1966, Habib 1976b). *A. cyperi* has not been reported as a competitor with *Bactra* spp. and, in fact, Poinar (1964b) reported that infested plants contained either species alone but not both. Thus the effect of *A. cyperi* is added to that of *Bactra* spp.

Habib (1976a, 1977) made a number of suggestions for introductions designed to increase effectiveness, which had been unsatisfactory in previous introductions. Because her work showed that *B. minima minima* and *B. venosana* are sympatric species that are capable of coexistence, apparently having different ecological preferences, she suggests the release of both species of *Bactra* with *A. cyperi* as one method to improve effectiveness. Such a combination has been tried on a small scale in Barbados, Cook Islands, and Tonga (Habib 1976a). In the United States, she suggested the study of several species of weevil for possible introductions. Also, she suggests *B. verutana* as an addition to the biological control agents presently reported for *C. rotundus* in Asia and Australia (Habib 1977). *B. verutana* has been the most studied biological control agent in detail. *B. verutana* has also been augmented in the field, and the effectiveness of releases of larvae and adults has been evaluated by Frick (1982).

Augmentation of Indigenous Biological Control Agents

The rationale for augmenting an indigenous species that has not been thoroughly tested to determine its host-plant spectrum is that, when augmentation ceases, the population will revert to its former level in the fauna. *Bactra* spp. are therefore promising candidates for augmentation, because the larval feeding injury is conspicuous, their selection of host plants is limited, and none of the species is known as a pest of agricultural crops except for chufa (table 2). After studying *Bactra* spp. as potential biological control agents for *C. rotundus* in several parts of the world, a number of researchers have concluded that some form of augmentation is needed to increase effectiveness (Cevallos and Navia 1971, Habib 1976a, Frick 1978, Garcia-Baudin et al. 1979). Toward this objective, diets for *Bactra* spp. were developed in Spain by Garcia-Baudin et al. (1979), California by Sieckert et al. (1974), and Mississippi by Garcia and Frick (1975), and a technique for large-scale artifical culture was devised by Frick et al. (1983). Of these efforts at augmentation, Garcia-Baudin et al. (1979) reared *B. furfurana* and *B. lanceolana* through two generations, while a laboratory colony at Stoneville, Miss., has been maintained since September 1971. The results of greenhouse and field studies in augmentation, using specimens from the latter colony, will be evaluated at the end of the discussion of *B. verutana*.

The population on which this section is based is indigenous to Stoneville, Miss.[1] The species was first described in 1875 from Dallas, Tex. Heinrich (1926) described the var. *chrysea* from southern California, and that name has subsequently been used in studies in California (Jefferson and Humphrey 1964, Poinar 1964a, Keeley et al. 1970, Sieckert et al. 1974). However, Diakonoff (1964) considered the validity of this form to be dubious, and the surmised differences in the shape of the valva to be due to the position in the slide mounts. Based on his doubt, I will not be using the name *chrysea* when discussing the California research. Only one specific name has been synonymized with (that is, made equivalent to) *verutana* and that is *dasioma* Diakonoff, 1963, from southern Africa (Diakonoff 1964).

Distribution

B. verutana is widely distributed; it has been reported from three continents. In North America, Diakonoff (1964) identified it from Florida, Texas, and California as far north as Placer County and from Baja California Norte in Mexico. Keeley et al. (1970) noted that the species has been collected from as far north as Butte County in California. Heinrich (1926) added the States of North Carolina, Mississippi, Louisiana, Missouri, and Indiana and the Provinces of Alberta and Ontario, noting that the species occurs rarely in northern localities. In the Caribbean region and Central America, it has been reported from Cuba, Puerto Rico, Panama (Diakonoff 1964), and Barbados (Habib 1977). In South America, *B. verutana* has been identified only from Paraguay, and in Africa from Cape Province and Natal, Republic of South Africa.

Host Plants

Recorded Species

The host plants of *B. verutana* may be divided into two groups: those found in nature and those determined through testing. In the first group are four species of *Cyperus,* one of *Scirpus* (Cyperaceae), one species of *Juncus* (Juncaceae), and a single record from the grass *Panicum dichotomiflorum* (Gramineae) (table 2). *B. verutana* thus has the broadest natural host-plant spectrum known for *Bactra* species.

Experimental Host Plants

Through the kindness of John Simmers, Environmental Effects Laboratory, U.S. Army Corps of Engineers, Waterways Experiment Station, Vicksburg, Miss., I obtained propagules of six *Cyperus* spp. from southern Illinois and of *C. esculentus* var. *sativus* from a commercial planting in Alabama. All were quickly and heavily attacked when exposed to *B. verutana* adults in a greenhouse (table 3). The results show a broader host-plant spectrum within the genus *Cyperus* than was previously suspected, which indicates that further testing surveys will probably reveal additional host plants within the family Cyperaceae.

Three grasses were tested in a greenhouse as hosts of the first-instar larvae (table 3). Rice, *Oryza sativa* L., and sudangrass, *Sorghum sudanense* (Piper) Stapf, were selected because both had been tested in Pakistan with *B. minima minima* and *B. venosana*. Fall panicum was included because of its record as a host in Virginia (Beisler et al. 1977). There was no feeding on these three grasses.

Two dicotyledonous plants were tested in a greenhouse in 1981–82 as potential hosts of 10-day-old (third-instar) larvae (Quimby and Frick 1985). Cotton, *Gossypium hirsutum* L., was included because of its being a common crop in the mid-South. However, when cotton is in the seedling stage in the spring, there would be virtually no half-grown larvae in nature (Frick and Garcia 1975). Turnip, *Brassica rapa* L., was selected as a representative of fall-planted crops in the mid-South. These crops are planted at a time when the larval population of *B. verutana* would be high (Frick and Garcia 1975).

Young cotton plants, usually with one small leaf but sometimes with two, were exposed to 10-day-old larvae wandering in search of a suitable food plant (table 3). Of 81 plants exposed, only 6 (7.4%) were injured, and 2 (2.4%) were killed. Damage consisted primarily of boring into the stem, either at soil level (two instances, one killing the plant) or at or near the growing tip (five instances, one killing the plant). The boring damage

[1]Identified in September 1971 by D. R. Davis, U.S. National Museum of Natural History. Voucher specimens are on deposit in the insect collection of the Department of Entomology, Mississippi State University, R. L. Brown, museum director.

varied from holes in the stem about 1 mm diameter to tunnels 8 to 10 mm in length. The tunnels killed varying numbers of leaves and cotyledons, and one killed all leaves and cotyledons, resulting in the death of the plant. In one instance, injury was confined to feeding between two leaves that the larva had webbed together.

Turnip plants were apparently in a vulnerable stage of development when infested at 2 weeks of age and were more heavily attacked than was cotton. Each plant generally had three or four leaves at least 23 mm in length. Each plant was infested by placing six first-instar larvae on the leaves with a small brush or by placing open 30-mL diet cups, each containing three third-instar larvae, near the plants. All plants were held for 14 days following infestation.

Newly emerged larvae damaged 39 of 40 turnip plants (table 4). There were four kinds or locations of injury following infestation: 23% of the feeding attempts were in the form of "nibbles" or circular scars 1 mm in diameter; 64% were leaf mines an average of 4 (range 1–15) mm in length; 8% were mined cotyledons; 5% were cotyledons or leaves about 25 mm in length killed by tunneling in the petioles. Most feeding occurred in the first 48 h following infestation, and there was no evidence of new feeding after 5 days, although a few living larvae were still observed on the plants, some in the second instar. A number of larvae were visible in their leaf mines, where some died within 5 days of infestation. The plants were examined 14 days after infestation. None of the injuries was of recent origin, nor had any of the growing tips been damaged detectably. The average number of leaves per plant was unaffected.

Ten-day-old larvae damaged 38 of 40 plants (table 4). Some growing tips were killed, which prevented the development of new leaves. Usually, however, injury was less severe, with the result that some stunted new growth was produced. Some larvae bored into and down the main stem, which killed the entire plant; others mined a petiole, killing its leaf. Leaf feeding was the least common injury, and it was confined to situations where two leaves touched or where one leaf touched the soil or edge of a container.

These results show that 10-day-old larvae of *B. verutana* feed under stress, 18% to the point of pupation and subsequent moth emergence, on young, actively growing plants that are phylogenetically unrelated to the Cyperaceae. Newly emerged larvae of *B. verutana* nibbled, mined, and tunneled in leaves, cotyledons, and petioles for up to 5 days in turnip plants after which no feeding was observed. The succulence of the young turnip plants was probably a factor in these attempts to feed.

Table 4—*Percentage of injury by type in 2-week-old turnip plants infested by* B. verutana *larvae* [1]

Type of injury	Amount of injury (%) by larvae infesting at—	
	1 day old	10 days old
Plants with leaf or cotyledon feeding only	95	8
Plants with feeding in petioles only	5	0
Plants with feeding in growing tips only	0	37
Plants killed	0	55

[1]Number of larvae per plant—larvae 1 day old, 6; larvae 10 days old, 3. Number of plants damaged out of 40—larvae 1 day old, 39; larvae 10 days old, 38. Larvae surviving to pupation—larvae 1 day old (fed a maximum of 5 days), 0%; larvae 10 days old, 18%.

Importance of Non-Host-Plant Feeding

The feeding behavior just described of *Bactra* larvae on grasses or on plants phylogenetically removed from the Cyperaceae might be termed "survival" or "maintenance" feeding. Such feeding is done under stress and in an attempt to prevent starvation. In nature, when in the presence of their host plants, *Bactra* larvae have not been observed to feed on such plants, with a single exception—fall panicum. Other than fall panicum, the reported host plants of *Bactra* larvae worldwide are in the families Cyperaceae, Juncaceae, and Typhaceae (table 2).

In addition, these trials confirm that the first- and third-instar larvae of *B. verutana* were similar in their feeding behavior to that of other species of *Bactra*. Poinar (1964b) was the first to note that "the data gained from the larval trials [with *A. cyperi* Marshall, a weevil] suggest that, as with the moth [*B. venosana*],

later larval instars can complete the remainder of their development on a wider range of plants than can the first instars." In Pakistan, studies with both *B. minima minima* Meyrick and *B. venosana* showed that, with both species, third-instar larvae had both greater feeding responses and completion of development to the adult stage on a wider variety of host plants than did the first-instar larvae (Ghani 1975, Habib 1976a).

The greenhouse tests previously described were followed with a field trial to test the susceptibility of fall-planted crops to attack by larvae of *B. verutana*. There were three replications of four-row plots, each 4 m wide by 12.2 m long, situated in a field having a high infestation of purple nutsedge. On September 10, 1982, seeds of spinach, *Spinacea oleracea* L.; radish, *Raphanus sativa* L.; and turnip were planted.

Daily applications of newly emerged larvae were started on September 20, produced as described by Frick et al. (1983), and mixed with corncob grits and distributed as described by Frick (1982). At the end of 2 weeks, an average of 35 larvae/ft^2 had been introduced into the plots. On October 22, 3 weeks after the final release was made, the plots were examined for larval infestation. Purple nutsedge plant density averaged 26/ft^2 in both check and release plots. There was an average natural infestation of 9% in the uninfested plots, while the release plots had an average infestation of 30% (K. E. Frick, unpublished data).

The crop plants were examined once or twice a week throughout the trial. At no time was any feeding damage noted to occur to the three crops. Turnip seed in particular was erratic in germinating, and new plants continued to appear throughout the 5-week period, so plants of a potentially susceptible age were always present.

Therefore, based on the known host plants, the lack of reports of feeding on desirable plants in nature, and the limited feeding on nonhost test plants by larvae in the genus *Bactra,* I feel that the release of small larvae of *B. verutana* in an augmentation program poses no threat to crop or pasture plants. However, *B. verutana* should not be introduced into new locations until the completion of a thorough testing program designed to determine its definitive host-plant spectrum.

Biology

Life Cycle in the Humid Subtropics

The annual cycle of *B. verutana* has been studied primarily at Stoneville and to a limited extent in California (Poinar 1964a, Keeley et al. 1970). The studies reported here are based on the work at Stoneville, situated in the humid subtropical region of the United States. That region is characterized by hot, moist summers and generally mild winters and is a transitional zone "between the continuously warm climates and those where winter becomes a definite characteristic" (Heintzelman and Highsmith 1967). Winters are sufficiently cold that all larvae and pupae exposed because of cultivation to the ambient air temperatures died; all large larvae near or below the soil surface died, but 11%–15% of pupae survived (Frick and Garcia 1975). The adults, eggs, and smaller larvae generally disappeared with the first killing freeze in the fall, as leaves and fascicles above ground died. Frick and Garcia (1975) showed in laboratory tests that, after 7 ± 1 days of exposure to 0 °C, about 66% of either field-collected or laboratory-produced eggs survived, as did 25%–27% of first- and second-instar larvae, 20%–40% of fourth-and fifth-instar larvae, and 40%–60% of pupae. Even though female moths held in the laboratory for 10 days at 0 °C were alive and able to fly, and 66% of field-collected eggs could survive for up to 10 days (Frick and Garcia 1975), the lack of available aboveground plant parts precludes activity after the first killing freeze of each fall, which occurred between October 24 and December 7 from 1971 to 1982.

Purple nutsedge begins to appear above ground in very late March or early in April at Stoneville, following which growth is rapid. *C. rotundus* is well known for its ability to rapidly reproduce vegetatively. Because of the prolific growth of the plants, the small overwintering population of *B. verutana* does not increase rapidly enough to be effective (Frick and Garcia 1975). With each generation requiring about 30 days, it is not until mid or late August that more than 50% of the plants are attacked. Thus, damaging populations of *B. verutana* appear about 4 months too late in the season to provide effective early season control. By mid to late September, from 80% to 95% of all shoots are attacked, showing that by the end of the season, *B. verutana* can approximately match the growth of *C. rotundus*. With a generation taking about 30 days, it requires about six generations for the insect to catch up with its host plant.

In general, Keeley et al. (1970) found a similar pattern of seasonal plant growth and slow increase in the *B. verutana* population occurring in California, although climate and species of nutsedge differ from those just described. The southern San Joaquin Valley, where the studies were conducted, is infested with yellow nutsedge, *C. esculentus,* and has a Mediterranean or dry summer subtropic climate characterized by mild, rainy winters and hot, dry summers (Heintzelman and Highsmith 1967). The host plant begins to grow in late February or early March, but it was not until early May that infested plants were noted. The numbers of infested plants remained low until early July, when a noticeable increase of infested shoots occurred. Thus, as in Mississippi, a significant population of *B. verutana* occurs about 4 months after the start of plant growth. In August, infestations varied from 13% to 52% for small plants less than 25 cm in height and from 31% to 84% for taller plants. The population level appeared to be at its highest in October when the percentages of infestation varied from 84% to 95% for small plants and 79% to 100% for large plants. Poinar (1964a) found infestations in *C. esculentus* at several places in southern California to vary from 22% to 50% in November and from 17% to 64% from late December and January. Infestations of *C. rotundus* varied from 54% to 100% from early November until late December. The severity of infestation throughout the growing season is not reported.

At Stoneville, the population of *B. verutana* decreased in October and November somewhat more rapidly than the host plant, as evidenced by a reduction in the percentage of infested plants and the number of eggs per plant. The latter was measured by the increase of time required to collect 50 egg-bearing plants: 1 h on September 13 and 3 h on October 15 and 16 and November 12, while on November 29, 3 h were required to collect 25 egg-bearing plants. The average number of eggs per egg-bearing plant also decreased, from 7.7 on August 21 to 1.8 on November 29 (Frick and Garcia 1975).

Stages in the Life Cycle

Egg Stage

The egg is subcircular, about 0.75 by 0.6 mm in diameter, flattened, and white when laid. As the egg develops, it first turns yellow, then the dark head of the embryo appears (fig. 1). Eggs ready to hatch are black to the naked eye. The eggs develop quite rapidly under a 12-h photophase at 32° ± 1 °C and a 12-h scotophase at 26° ± 1 °C, requiring only 2.5–3 days from oviposition to eclosion (Garcia and Frick 1975). The eggs are laid on the leaves of the host plant, primarily on the upper surface.

The egg stage withstood immersion in water for 2 h with no loss in viability, but immersion for 48 h caused a 27% reduction in eclosion (Frick and Wilson 1980). Thus, the eggs appear to be adapted to survive the occasional heavy rains (25–50 mm) that can occur during a summer thunderstorm. On the other hand, dry conditions reduce eclosion. For example, Frick and Wilson (1980) found that in the laboratory, the percentage of eggs that eclosed increased significantly (by 31%) from 0% to 50% RH. In a hot (average maximums 35° ± 3 °C, average minimums 30° ± 2 °C) greenhouse in which daytime relative humidity averaged 50% to 60% and nighttime, 80% to 90%, egg-bearing plants were clipped and laid out to dry. Eclosion after 0, 1, 2, 3, and 4 days averaged 73%, 24%, 9%, 4%, and 0% respectively. In contrast, in a temperature cabinet under a 12-h photophase at 32° ± 1 °C and 12-h scotophase at 26° ± 1 °C, and at slightly lower humidities, eclosion averaged 79%, 68%, 68%, 58%, and 63%, respectively, over the same period. These two tests, while not strictly comparable, do indicate that the extreme temperatures in the greenhouse (air plus radiation from the sun) were a factor in the increased egg mortality obtained there.

Larval Stage

On the basis of preliminary data, Frick and Garcia (1975) reported that there were five larval instars. Later, in a detailed study of individual larvae, it was determined that there were four, five, or six instars involved during development (Frick and Wilson 1978). Larvae reared on the host plant had a higher percentage of four-instar larvae (35%) and smaller percentages of five-instar (58%) and six-instar (7%) larvae than larvae reared on diet, which had only 4% of four-instar larvae but 79% of five-instar and 17% of six-instar larvae. That fewer instars were required for development on the host plant indicates that the host plant was the more satisfactory food source. The greater the number of instars, the smaller the size of increase at each molt (Frick and Wilson 1981). Each molt of four-instar larvae increased width of the head capsule by one-third, five-instar larvae by about one-fourth, and six-instar larvae by about one-fifth. However, head capsule

measurement was found to be an unreliable method of determining larval instar after the second molt or of determining whether a larva will require four, five, or six instars to complete development. The total duration of the larval instar varied with the number of instars required for maturity: 11–13 days for four-instar, 15–17 days for five-instar, and 21–23 days for six-instar larvae (Frick and Wilson 1978).

Upon hatching, the larvae generally migrate to the central, most immature leaves of the whorl at the upper end of the stemlike fascicle. Most of the feeding damage is not obvious for a number of days, because the larvae generally feed between these appressed leaves. Feeding damage consists of removal of the palisade parenchyma and mesophyll and leaving of the lower and sometimes the upper epidermis. Frick and Wilson (1978) found that the average length of these damaged areas was 8.7 mm (range 1–30), while the width was the same as the width of the larva. The upper epidermis was left intact (mining) in about 50% of the plants, but it was consumed (skeletonizing) in the other 50%, particularly where two leaves were pressed tightly together. However, individual larvae also made a few scattered mines on the mature leaves. In one test, an average of 1.9 mines was found on 31% of the leaves of small shoots, which averaged six leaves each. Measurements of such isolated mines revealed that they averaged 8.0 mm (range 1–21) in length. In addition, nibbling—circular areas less than 0.25 mm diameter—was present and accounted for as much as 31% of the total number of separate instances of feeding damage.

Mining or sketetonizing continued for 4 days, after which larvae began to feed down into the fascicle. On the sixth day, the larvae took either of two routes to reach the base of the fascicle. They (1) migrated down through the fascicle or (2) bored out of the fascicle and reentered farther down. In a total of 45 mature shoots, 52% of the larvae left the upper portions of the fascicles to reenter nearer the soil surface. Reentry was frequently begun at the base of the more mature, lower leaves. The larvae sometimes entered at the collar where the leaf breaks away from the fascicle, or, more frequently, they fed downward between the outermost leaf sheath and the fascicles for an average of 8 mm (range 5–12) before boring into the center of the fascicle at an average of 25 mm (range 0–58) above the soil surface.

On the sixth day, the first indications of deadheart became evident. The term "deadheart" is used to describe the appearance of a shoot after 1–4 of the most immature, central leaves at the tip of the fascicle have died. On the seventh day, 90% of the larvae were feeding on the lower one-half of the fascicle, with about 10% of these feeding at the top of the basal bulb. Most larvae reached the basal bulb on the eighth day. Upon reaching the bulb, 44% of the larvae left the fascicle to seek a second shoot, moving an average of 36 mm (range 2–90) to reach it and often bypassing nearer shoots. Second shoots were bored into at 19 mm (range 5–35) above the soil surface. This entry hole sometimes also served as the hole from which the larva then pushed its fecula and from which the pupa subsequently protruded at the time of moth emergence. The height of the pupal exit hole above the top of the soil averaged 10 mm (range 0–32) as measured on 35 shoots. The fascicles were most heavily fed on between the bulb and the pupal exit hole, which averaged 30 mm (range 20–45) in distance.

In the greenhouse tests in which a single larva was placed on 1 of 12 shoots in individual trays, all injured shoots were removed and examined for damage. The basal bulbs of the injured shoots in 20 of the trays were dissected, and the amount of damage caused by each larva was estimated. The larvae that completed their feeding in a single shoot consumed approximately 15% (range 5%–25%) of each basal bulb. The larvae that entered a second shoot fed on its bulbs an estimated average of 16% (range 5%–33%). These percentages varied widely and were due, at least in part, to varying fascicle diameters and lengths—the latter depending on the depth of the basal bulb beneath the soil surface.

Based on observations made under unnatural conditions in the laboratory, Frick and Garcia (1975) noted that the larvae were cannibalistic. However, in subsequent studies, it has been shown repeatedly that all instars are mobile and disperse from overcrowded conditions, but before they do, they tend to avoid each other while inflicting increased damage on their host plant. Frick and Wilson (1978) found that, after 3 days, 17% of 10 first-instar larvae per small shoot had left their respective shoots. Of these, 72% were dead on the sides of the plastic bags. In contrast, 8% of the single larvae per small shoot were dead on the bags.

By the 10th day, 43% of 250 larvae (25 bagged shoots) had left their shoots and were on the plastic bags, 27% of them dead. In contrast, only 20% of the single larvae had abandoned their shoots: three were dead and two were lost.

Attempts to account for all larvae on the small shoots were only partially successful, because the larvae quickly became crowded as a result of the extensive feeding damage, and they dispersed while still small. Frick and Wilson (1978) were more successful in accounting for all the larvae in the two tests, by using large shoots. In the five bags with a single larva, four larvae became adults and one died in the fascicle. In the case of five larvae applied per shoot, 32% died as larvae off the shoots between days 5 and 13, and four mature larvae and pupae (16%) were found dead in the fascicles on days 17 and 19. None of the insects showed any evidence of external injury. Thirteen moths (52%) emerged from these five very large shoots (5–6 mm fascicle diameter), with two to three moths issuing from each shoot. Thus, this test showed that, when not overcrowded to the point of destroying their host plant, several larvae could complete the last two or three instars in a single shoot.

When 10 newly emerged larvae were used on each of 6 large shoots, no larvae were seen off the shoots until the sixth day when 1 dead larva was found on a bag. On the 10th day, 20% of the larvae were crawling on the bags. These larger larvae, seen from day 7 through day 18, were able to escape from the plastic bags by chewing small circular holes in them, primarily at the top where each was held together tightly with a rubberband. In fact, 90% of the larvae escaped, and an average of nine holes per bag was found. Of the remaining 10%, one was dead on the sixth day, and five pupated. All 10 larvae escaped from 1 completely deteriorated shoot. Each of the single larvae completed development without leaving its shoot.

Infestations of purple nutsedge shoots of various ages with newly emerged larvae showed that shoots 5 and 6 weeks old were unacceptable to the larvae, and only about 20% of 4-week-old shoots supported larval development to pupation and adult emergence (Frick and Wilson 1980). Ninety-two percent of the larvae completed development on 2- and 3-week-old shoots.

Frick and Wilson (1980) felt that these results supported their field observations that mature or senescent plants are not selected for larval feeding. Thus, such patches of aging plants do not contribute to the build-up of a population of *B. verutana* unless destroyed by cultivation, following which the new growth may be readily attacked. Frick and Wilson (1980) found, for example, that a portion of a field of purple nutsedge shoots, 90% of which were infested with larvae of *B. verutana,* was disked in two directions to a depth of 10–15 cm on July 20, 1979. Twenty-one days later, there was a heavy growth of 400 new shoots/m^2. At that time, 89% of the shoots were infested, with 18% of those shoots showing deadheart. Thus, young, vigorous shoots can be rapidly infested in midsummer following cultivation.

A thorough disking can destroy many larvae, as was shown by the numbers of moths subsequently seen in field cages over a 25-day period. In the undisturbed portion, 47 moths were sighted, an average of 24 moths/m^2. In the disked portion, only four moths were sighted, a reduction of 91%. Thus, disking of vigorous, young shoots of purple nutsedge is harmful to *B. verutana* larvae and probably pupae, but disking of mature or senescent shoots is beneficial to *B. verutana* because an ample supply of plants regrow and are suitable for oviposition within 2–3 weeks.

Although the cultivation test showed that *B. verutana* could rapidly reinfest its host plant in midsummer, could the insect accomplish the same thing at the lower temperatures prevailing in mid-May and mid-June when natural populations are low? Would augmenting the natural population with large numbers of larvae result in increased plant damage at the reduced early season temperatures? To answer these questions, a laboratory test was designed to determine damage at the average high and low temperatures of mid-May (24 °/13 °C), mid-June (29 °18 °C), and mid-July (32 °/26 °C). The relative amounts of damage resulting from larval feeding were similar at all temperatures (Frick et al. 1978). Thus, the effects of the slower developing larvae feeding on the slower growing *C. rotundus* at the lower temperatures were proportional to the effects of the faster developing larvae feeding on the faster growing plants at the mid-July temperature. Because of this, *B. verutana* larvae have been able to provide control of *C. rotundus* when put in the field during May and June at the prevailing temperatures (Frick and Chandler 1978).

Pupal Stage

At the time of pupation, the pupa is usually green, retaining some of the color of the mature larva. However, the pupae soon turn tan and darken with maturity to brown. The pupal stage is about 1 week long. Poinar (1964a) reported 6–8 days at 24 °C, while Frick and Wilson (1978) showed a pupal life of 7 ± 1 days at 28 ° or 29 °C, regardless of sex or the number of larval instars. Live pupae obtained from *C. rotundus* plants growing in the field averaged 14.7 mg in weight (Frick et al. 1983). The pupae of female moths averaged 1.5 times larger than the pupae of male moths (17.8–11.6 mg). This ratio of female : male weights remained the same when larvae were reared on diet, which increased the average weight and size. The diet of Garcia and Frick (1975) increased the average pupal weight only to 1.1 times that of the field-collected pupae, while three subsequent, improved diets increased average pupal weights 1.2 and 1.4 times (Frick et al. 1983).

Pupation occurs in the fascicle, which the larva has hollowed out; it has lined the tunnel with a silken tube. At the top of the tunnel, the larva provides an exit hole through which the mature pupa partially exits just before moth emergence. The height of the pupal exit hole above the top of the soil averaged 10 mm (range 0–32) (Frick and Wilson 1978). For maximum emergence, the pupae require a rather high relative humidity. For example, in a laboratory test, moth emergence was 92%–96% from pupae held at 90%–100% RH, 49%–74% emerged at 11%–80% RH, while 35% emerged at 0% RH (Frick and Wilson 1980).

Adult Stage

The adults are small grayish moths with a wing length between 4 and 9 mm when they have been reared continuously on their host plant (Frick and Wilson 1982) (fig. 4). The males tend to be smaller, averaging 6.0 ± 0.5 mm (range 4.8–6.9) in wing length, while the females average 6.9 ± 0.6 mm (range 5.6–8.5). Males are overall darker gray, with several pairs of large oblong brownish-black spots on each forewing. These spots are about 1.5–2.0 mm long by 1.0 mm wide (fig. 5). The females are lighter gray, and the smaller spots on the forewings are about 1.25–1.5 mm by 0.75 mm (fig. 5).

The moths are active at night and are seen flying in daytime only if disturbed. In direct sunlight, such flights were short and rapid with a quick return to the host plant (Frick 1982). With the approach of thunderstorms when it was relatively dark and humid, about 5% of the moths flew in sustained flights, and 15% flew 3–5 m when disturbed. The moths flew only slightly more readily between sunset and nightfall before total darkness. After dark, the flight pattern generally changed to sustained flights with some hovering before alighting. Mating occurred at night or as dark broke. Although oviposition has not been observed in the field, it occurs during scotophase in the laboratory.

A field study was designed to determine the placement of eggs on the host plants. Plant samples of *C. rotundus,* collected on August 21, 1973, at about the height of moth activity, were selected because of one or more eggs on the upper surface of a leaf. The average number of eggs per plant in two 25-plant samples was 6.8

Figure 4.—Newly emerged female moth of *B. verutana*.

Figure 5.—*B. verutana* adults, female on the left, male on the right.

and 8.6, of which 59% and 69%, respectively, were on the upper surface (Frick and Garcia 1975). Between August 21 and November 29, 1973, eggs became more scarce as evidenced by (1) the greatest number of eggs per plant decreasing from 23 to 6, (2) the average number of eggs per plant decreasing from 7.7 to 1.8, (3) the percentage of plants bearing 5 or more eggs each decreasing from 32% to 8%, and (4) the percentage of plants bearing one egg each increasing from 8% to 56%. Not all eggs on a plant were laid at the same time, although those in each cluster were. Therefore, the percentage of unhatched eggs varied widely—from 24% to 95%. Either the females do not produce an oviposition-deterring pheromone at the time of egg laying, or, if they do, it would appear to be very short-lived.

The first eggs (18%–30% of the total eggs laid) are usually laid on the third day following emergence (Garcia and Frick 1975, Frick and Wilson 1982). However, a few eggs may be laid on the second day of adult life. In one series of oviposition studies, 4% of an average 163 eggs per female were laid on the second day. The oviposition period can last 7 days (day 3 through day 9) (Garcia and Frick 1975). However, more than 90% of the eggs are laid in the first 5 days of oviposition (day 3 through day 7). Longevity of adults has been little studied because they are cleared out of the oviposition cages after 7 days—2 of preoviposition and 5 of oviposition—when egg laying is about completed (Garcia and Frick 1975, Frick et al. 1983). However, by providing a honey-sucrose solution for food and increasing the relative humidity to more than 80%, Garcia and Frick (1975) increased longevity to as much as 21 days.

Laboratory studies of female fecundity consistently resulted in 80%–90% viability of eggs (Frick and Wilson 1980, 1982). This was attributed to the 1:1 sex ratio maintained in the oviposition cages. This is based on the determination that 10% of 20 males did not mate and that, to obtain 80% or more viability, the females should mate by the time that they are 2 days old (Frick and Wilson 1982). Thus, surplus males should be provided in all oviposition cages in an attempt to increase viability.

The average number of eggs laid per female has fluctuated around 200, varying from averages ranging from about 150 to 250, and has depended on the conditions presented to the newly emerged moths (Frick et al. 1983). Some of these conditions include type of oviposition cage, smoothness or roughness of cage surface, numbers of pairs per cage, presence or absence of a bouquet of the host plant, female size, immediacy or delay of mating, and age of male. Of these, crowding appears to be the most important factor; this conclusion is based on the studies of Garcia and Frick (1975). A regression line was later calculated (Frick and Chandler 1978, Frick et al. 1979) on the results of these studies and of a separate study using host plants as the oviposition substrate (Frick et al. 1979). However, an entirely new type of cage was developed that appeared to minimize the importance of crowding (Frick et al. 1983). It had a cylindral oviposition frame of 3.1-mm-mesh hardware cloth wrapped with a single layer of clear polyethylene plastic food wrap for the substrate (fig. 6). This 3-liter cage held 50 pairs of moths. Eggs were laid down between the wire grid on the plastic wrap. Even though very crowded, each female averaged 257 ± 53 eggs.

Female size, as measured by wing length, is correlated with total dry weight (correlation coefficient = 0.85) and with the number of eggs laid per female (correlation coefficient = 0.82) (Frick and Wilson 1982). However, to obtain maximum fecundity, mating with a vigorous male is necessary. In the absence of mating, females laid an average of 27 infertile eggs (Frick and Wilson 1982). At a ratio of 1♂/8♀, the females averaged 41 eggs that were only 26% viable, while at 1♂/5♀, each female averaged 52 eggs that were 75% viable. Nine males produced their final spermatophore on day 5 ± 2. Of those, two-thirds fertilized the egg complement of virgin females while one-third deposited almost no viable sperm because each female laid an average of 30 eggs that were only 23% viable. Females

Figure 6.—Oviposition cage, 3 liter and 50 pairs of moths capacity, that increased egg production per female 21%–35%.

from 0 to 5 days of age when first mated showed no significant differences in fecundity, although there was a trend toward lowered viability with advancing age at time of first mating.

Modifying the Injury to the Host Plant

Studies of *B. verutana* as a potential biological control agent of *C. rotundus* have been concerned with increasing the insect's effectiveness. With natural populations of *B. verutana* remaining low through June in California (Keeley et al. 1970) and through July in Mississippi (Frick and Garcia 1975, Frick and Chandler 1978, Frick 1982), manipulation or augmentation to achieve high early season populations is necessary if this insect is to act as a biological deterrent to *C. rotundus*. Not only do damaging insect populations appear late in the season, but the larvae do relatively little real damage to this host plant. For example, late in the 1973 growing season, 68%, 73%, and 77% of infested plants produced new shoots from injured basal bulbs (Frick and Garcia 1975). These percentages compare favorably with those obtained in a greenhouse when 83% and 71% of injured plants of purple and yellow nutsedge, respectively, sprouted new shoots (Frick et al. 1979). In addition, each larva fed on an average 1.6 purple or 1.7 yellow plants of which 17% and 29% were killed—that is, the plants did not sprout new shoots. Therefore, during their development, 100 larvae have the potential to kill an average 27 purple or 49 yellow plants 14–18 days old. In a separate test, it was concluded that only 12% of 14- to 18-day-old purple nutsedge plants would be killed by the feeding of a single larva (Frick and Wilson 1978). In attempts to increase the damage caused by natural populations of *B. verutana,* studies were conducted in the laboratory, greenhouse, and field.

Laboratory Studies

The laboratory studies (Frick and Wilson 1978) consisted of comparisons of the plant damage resulting from the feeding of 1 vs. 10 first-instar larvae and 1 vs. 5 half-grown, probably third-instar, larvae. Three days after 1 or 10 neonate larvae were placed on small shoots about 15 cm tall and 3 cm in fascicle diameter, the average numbers of mines on mature leaves was 3 vs. 13, the percentage of mined leaves was 31% vs. 96%, and the percentage of whorls being fed on was 26% vs. 64%. After 7 days, the percentage of fascicles containing larvae was 41% vs. 100%. The percentages of plants abandoned by the larvae as unsuitable for further feeding were 25% vs. 33% after 7 days, 51% vs. 80% after 10 days, and 76% vs. 96% after 14 days.

Six days after 1 or 10 neonate larvae were placed on plants twice as large, the average percentage of leaves fed on was 41% vs. 81%, and the percentage of deadheart was 0% vs. 100%. Damage to the basal bulbs was not as extreme, with all bulbs sprouting new shoots during the pupal period. Following that, the shoots were removed and the bulbs replanted. Of those fed on by a single larva, 66% produced a second shoot compared with 33% of those exposed to 10 larvae.

Five days after one or five half-grown larvae were placed on large shoots, the average percentage of deadheart was 20% vs. 100%; at 8 days, 80% of the plants with a single larva had deadheart, and 100% of the others had collapsed and fallen over. Again, the basal bulbs were not as severely injured. Feeding by five larvae killed 20% of the bulbs; otherwise all of them sprouted new shoots.

To be effective, larvae should be released 2–4 weeks after crop planting while the host plant is only a few weeks old. Thus, releases would have to be made in May and June when temperatures are relatively cool. Because it was not known how active the larvae would be during those months, the test previously described was done to provide the average high and low temperatures of mid-May, mid-June, and mid-July. The relative amounts of damage resulting from larval feeding were similar at all temperatures (Frick et al. 1978). Thus, the effects of the slower developing larvae feeding on the slower growing *C. rotundus* at the lower temperatures were proportional to the effects of the faster developing larvae feeding on the faster growing plants at the mid-July temperature. Thus, early season release of larvae has the potential to cause sufficient damage to make field augmentation a success (Frick and Chandler 1978).

Greenhouse Studies

The effects of six different conditions of the host plant were studied. Feeding by three larvae per shoot reduced average dry weight of unfertilized plants by only 22% and that of fertilized plants by 30% and 42% (Frick and Quimby 1977). Plants under the osmotic stress

caused by adding NaCl to produce −8 bars of osmotic potential were reduced 31% in dry weight. Feeding by three larvae per plant reduced dry weight another 40%. Unstressed plants suffered an average 52% loss in dry weight from feeding. Thus, where fertilization significantly increased larval injury, osmotic stress did not increase or decrease percentage of damage.

Age is another factor in the suitability of a host plant for larval feeding. Where 92% of larvae completed development on 2- to 3-week-old plants, only 21% did so on 4-week-old plants, and none developed on 5- to 6-week-old plants (Frick and Wilson 1980). Repeated injury from larval feeding has increased damage and reduced plant dry weight (Frick and Quimby 1977). In one series of tests, one infestation of two neonate larvae per plant reduced dry weight by an average 51%, and two, three, and four weekly infestations further reduced dry weight 73%, 76%, and 81%, none of which were significantly different from each other (fig. 7). In other tests, single infestations reduced dry weight by 66% and 69%, four infestations by 77% and 83%, and eight infestations by 98% and 99%. Therefore, for best results, augmentative releases of larvae should be applied at least twice to 2- to 3-week-old, vigorously growing plants. A cultivation 2–4 weeks prior to the first release may be desirable to stimulate growth of the host plant.

Crowding of plants and multiple larval infestations are also involved in the severity of response to feeding damage. When an equal number of larvae per plant was compared at low density (5 larvae/1 plant/pot) vs. high density (45 larvae/5 plants/pot), tuber production

Figure 7.—Effects of multiple weekly releases of two neonate larvae per plant. From left to right, zero, one, two, three, and four releases.

after 6 weeks was significantly reduced at the high density (Frick et al. 1979). The numbers of tubers were reduced 36% at the low density and 77% at the high density, and tuber dry weight by 72% and 93%, respectively. Yellow nutsedge was also affected by crowding. Significant reductions at low and high densities were 68% and 94% for plant height, 44% and 62% for numbers of tubers per pot, and 47% and 80% for tuber weight, respectively.

Potted plants subjected to three periods of larval feeding during 13 weeks suffered significant decreases in both shoot and tuber production. Aboveground plant growth was reduced 27% in height and 80% in dry weight, while tubers were reduced 45% in number and 78% in dry weight (Frick et al. 1979). Yellow nutsedge responded similarly, with shoot height being reduced 42%, shoot weight 67%, and tuber weight by 49%, although the number of tubers produced were not significantly reduced.

Field Studies

Although the studies reported here were designed to determine whether host-plant damage could be increased, another study was concerned with reducing the damage caused by *B. verutana* (Jefferson and Humphrey 1964). In southern California, papyrus is a popular ornamental that is attacked by the larvae that feed on the leaves and bore into the stems and crowns. *B. verutana* caused severe damage in nurseries where young plants were stunted and seedlings killed. A satisfactory program of pesticide applications was developed to protect plants about 38 cm tall.

Also in California, Keeley et al. (1970) conducted a series of tests in 1967 designed to increase injury and reduce the plant growth of *C. esculentus*. Trays of uninfested plants were placed in field cages with either no *B. verutana,* a natural population of the insect, or a population induced by introducing infested plants. Percentages of infestation and damage inflicted depended primarily on the period elapsing between placing the test plants into the cages and their infestation. The highest infestation and significant reductions in numbers of new plants and tubers and in total dry weight occurred when the test plants were infested in 7–8 days. No significant reductions occurred when it took 21 days to become infested. Intermediate results were obtained when it required 14 days to achieve an infestation.

In Mississippi, releases of *B. verutana* into field plots were carried out over a 6-year period from 1972 through 1977 (Frick and Chandler 1978). In summary, 3 weekly releases of 5–10 neonate larvae per plant, beginning 3 weeks after crop planting, suppressed the aboveground growth of the purple nutsedge 50% ± 1% 6–7 weeks after the last release, while 4 or 5 weekly releases reduced purple nutsedge growth 62%–68% (figs. 8 and 9). However, there were no significant differences between three, four, or five releases in either host-plant suppression or yield of seed cotton. Such early season suppression of the weedy host plant significantly reduced its growth for 6–7 weeks, a sufficient period of reduced competition from the weed that, in the presence of *B. verutana* larvae, there was no significant reduction in yield of seed cotton compared with plots with no purple nutsedge. Although 3–5 releases each of 5–10 larvae per plant may appear excessive, it was observed that, in the absence of *B. verutana* larvae, there was an average fivefold rate of increase in plants per 3-week period so that after 6 weeks there was an average 25 plants for each 1 present at the start. Thus, in spite of the number of larvae required, augmentation of populations of *B. verutana* in the form of early season releases showed promise as a method of controlling purple nutsedge.

Based on the results of Frick and Chandler (1978), Frick (1982) conducted larger scale augmentative field releases of both adults and larvae. Preliminary releases of adults in 1977 and 1978 confirmed results obtained in the greenhouse that mature plants of *C. rotundus* are not selected for oviposition, plants about 4 weeks old are about 20% infested, and 2- to 3-week old plants are preferred (Frick and Wilson 1980). In six plots in cottonfields, from two to four weekly releases of adults were made in 1979. Totals of 4,800–8,100 moths were released over the 3-week period, but dispersion was limited from the points of release where infestations were from 93% to 100%. Considering that at least 50% of the plants must be infested to provide for a significant reduction of the weedy host plant (Frick and Chandler 1978), effective control was restricted. Thus *B. verutana* adults proved effective in circles only 5 m in radius in five of the sites and out to 10 m in the sixth site. By way of comparison, natural infestations in neighboring fields varied between 3% and 4%. At the distances from 6 to 30 m away from the points of release, there was a twofold to twelvefold increase in infested plants over the natural infestations of 3% and 4% in neighboring fields.

Figure 8.—Growth of *C. rotundus* in cotton in the absence of *B. verutana* 8 weeks after the tubers were planted on May 14, 1976.

Figure 9.—Growth of *C. rotundus* in cotton 8 weeks after the tubers were planted on May 14, 1976, and 3 weeks after the last of 3 weekly releases of 5–10 *B. verutana* larvae per plant.

Results of broadcast releases with neonate larvae mixed in corncob grits all indicated that dispersal after release is limited and that larval effectiveness is enhanced by high host-plant density. For example, at the greatest density (37 plants/ft^2), 52% of the larvae infested a plant, while at the lowest density (17 plants/ft^2), only 6% of the larvae attacked a plant. Infestations resulting from a single release in each of four plots in 1979 varied from 24% to 67%. At the same time, the natural infestations in nearby plots varied from 18% to 41%. In 1980, infestations at 10 sites following 3 or 4 releases varied from 34% to 94%, while natural infestations at 10 locations in nearby fields varied from 1% to 10%.

In summary, newly eclosed larvae mixed in corncob grits appear to be the preferred method of release. However, regardless of the stage of *B. verutana* at release, the ultimate success of any augmentation depends on the age and condition of the plants. High rates of infestation are possible only when most of the shoots are in a vigorous growing condition 10–21 days after cultivation. Thus, the chance for the success of an augmentation is increased if the target area is cultivated 10–14 days before the first release is planned.

Comparison of World Ecotypes

A total of 38 ecotypes of *C. rotundus* were made available, 22 from locations scattered around the world plus 16 from the coterminous States of the United States. Six tests were conducted with these ecotypes, three in 1979, ending on September 6 and 26, and three in 1980, ending on September 30, October 30, and December 18. The various methods used are given in table 5. Three different criteria were selected for evaluation in 1979, so each evaluation is considered separately. Test 1979–A (and all three of the 1980 trials) consisted of estimating the percentage of injury (reduction in plant growth) by comparing it with that of uninfested plants of the same ecotype. This was done because of the different habits of growth exhibited by many of the ecotypes. Test 1979–B was an estimate of the percentage of injury done to the damaged plants only and ignoring any uninfested plants. For test 1979–C, an actual count of the injured and dead plants was made and the percentages of those plants to the total number of plants per pot were then used for the analysis of variance. The experimental units of two or three replications each were arranged in a randomized complete-block design. All tests were conducted in a greenhouse without artificial light. Temperatures ranged between 25° and 40°C. All percentages of damage were transformed into the arcsin percentage for analysis of variance except for test 1979–A. After the analyses of variance were completed, means were compared according to Duncan's new multiple-range test at the 5% level.

The results of the three combined 1980 evaluations and the three 1979 tests are given in table 6. Ecotypes were not all attacked to the same degree, nor were the degrees of infestation consistent within an ecotype.

Because of these variations, it may be assumed that *B. verutana* at Stoneville, Miss., would attack most of the ecotypes at least as heavily as it damages the Stoneville ecotype, which generally ranked rather low (table 6). But, before *B. verutana* is released in another country, it should be tested on the local ecotypes of *C. rotundus,* not only in comparison with any local *Bactra* spp.,

Table 5—*Methods and conditions under which the world ecotype comparisons were conducted*

Test No.	No. of replications	Date plants clipped	Method	Date	Infestation or clipping to evaluation days	Evaluation	
						Date	Method
1979–A	3	7/26	3 neonate larvae/pot (10 cm diam)	8/14	24	9/6	Estimated % injury to each ecotype compared to its own untreated check
1979–B	3	7/26	3 neonate larvae/pot (10 cm diam)	8/14	24	9/6	Estimated % injury to infested plants only
1979–C	3	9/6	2d-generation adults		21	9/26	Percentage of dead and injured plants per pot
1980–1	3	9/2	3 neonate larvae/pot (10 cm diam)	9/4	27	9/30	Estimated % injury to each ecotype compared to its own untreated check
1980–2	2	10/1	5 neonate larvae/pot (10 cm diam)	10/7	24	10/30	Same
1980–3	2	10/30	2d-generation adults		50	12/18	Same

but also in comparison with the two well-studied species of *Bactra* in Pakistan—*B. minima minima* and *B. venosana*.

Table 6—*Results of 3 combined evaluations made in 1980 of 38 ecotypes of* Cyperus rotundus *L. compared with 3 different evaluations made in 1979 of 35 ecotypes*

Geographic location	1980 Series		1979-A		1979-B		1979-C	
	Rank	Estimated overall injury (%)	Rank	Estimated overall injury (%)	Rank	Estimated overall injury (%)	Rank	Estimated overall injury (%)
Tanzania	1	95a	22	22c-f	19	59d-g	20	93.9a-c
Iran	2	89ab	24	20c-f	20	57d-g	26	92.9a-c
Sudan	3	86 a-c	9	33b-e	22	56.7d-g	28	92.1a-c
Malaysia	4	79a-d	27	18c-f	4	74b-d	3	100a
Israel	5	77a-d	1	62a	10	64b-g	22	93.1a-c
Greece	6	73a-e	3	53ab	6	70b-e	34	85bc
Indonesia	7	68a-f	29	12ef	35	43g	1	100a
Philippines	8	68a-f	28	17df	7	66b-f	33	87a-c
Argentina	9	64b-f	11	33b-p	34	43g	7	99.2a-c
Japan	10	63b-f	25	20c-f	1	98a	17	95a-c
U.S. (Plains, Ga.)	11	62b-f	19	23c-f	32	47fg	30	91a-c
U.S. (Raleigh, N.C.)	12	60b-f	31	12ef	26	54d-g	12	98a-c
U.S. (Oahu, Hawaii)	13	59b-f						
Mauritius	14	58b-f	12	30b-f	28	53d-g	21	93.8a-c
U.S. (Shafter, Calif.)	15	57b-f	18	23c-f	9	66b-f	24	93a-c
U.S. (College Station, Tex.)	16	54c-f	4	53ab	30	48e-g	6	99.3ab
Thailand	17	52c-f	22	22c-f	27	53d-g	15	96.3a-c
U.S. (Phoenix, Ariz.)	18	51c-f	2	53ab	7	67b-f	27	92.3a-c
Brazil	19	50d-f	7	38a-d	13	63.4b-g	2	100a
U.S. (Knoxville, Tenn.)	20	47d-f						
U.S. (Palmerdale, Ala.)	21	46d-f	14	27c-f	18	60c-g	10	99.1a-c
New Zealand	22	45d-f	20	23c-f	31	47fg	14	96.9a-c
U.S. (Houma, La.)	23	45d-f	34	10ef	33	45fg	16	96.2a-c
Australia	24	44d-f	33	10ef	24	54d-g	13	97a-c
El Salvador	25	42d-f	5	43a-c	16	60c-g	25	93ac
Western Samoa	26	41d-f	26	20c-f	29	50e-g	4	100a
U.S. (Orlando, Fla.)	27	40.6d-f	7	33b-e	3	79bc	19	94.4a-c
Taiwan	28	40.3d-f	32	12ef	22	56.7d-g	29	91.6a-c
U.S. (Stoneville, Miss.)	29	39.7d-f	15	27c-f	29	60c-g	31	90a-c
U.S. (Saint Joseph, La.)	30	39.2d-f	30	12ef	21	56.8d-g	22	93.2a-c
U.S. (Little Rock, Ark.)	31	36ef	10	30bf	5	74b-d	5	100a
U.S. (Clemson, S.C.)	32	35.7ef	35	7f	14	62c-g	32	89a-c
Puerto Rico	33	35.3ef	6	43a-c	2	81b	7	99.3ab
Trinidad & Tobago, Trinidad	34	34ef	16	27c-f	25	54d-g	25	79c
Colombia	35	31f	17	25c-f	15	60c-g	18	94.9a-c
U.S. (Jackson, Tenn.)	36	30f	13	30b-f	12	63.6 b-g	9	99.2a-c
U.S. (Las Cruces, N. Mex.)	37	29f						
U.S. (Weslaco, Tex.)	38	28f	21	23c-f	11	63.9b-g	11	99.1a-c

[1]Within columns, numbers followed by the same letter are not significantly different according to Duncan's new multiple-range test ($P=0.05$).

Methods of Manipulation and Augmentation

In a humid subtropical climate, where winter is devastating to the population of *B. verutana,* only small numbers of the insect are available to attack the flush of spring growth of *C. rotundus*. Growth of the host plant is particularly rapid for 6 weeks following crop planting. An average growth rate of fivefold per 3 weeks has been reported during this period (Frick and Chandler 1978). Thus, there can be 25 plants at the end of 6 weeks for each 1 present at the start—and that at a time when the numbers of *B. verutana* are at there lowest (Frick and Garcia 1975). Because of these factors, the only method of population manipulation that appears to be feasible is that of augmentation by means of mass rearing and release in the spring, beginning 1–2 weeks after crop planting (Frick 1978).

Releases of laboratory-cultured *B. verutana* can increase the rate of infestation of *C. rotundus* with the right combination of growth stage of the plants and how close the insects are released to the target weed (Frick 1982). The *B. verutana* culture used for the tests reported here was obtained from the population at Stoneville, Miss., in the Lower Mississippi Valley, and it appears to be well adapted to an agroecosystem. This native population is virtually immune to toxaphene (chlorinated camphene containing 67%–69% chlorine) with no deaths among the moths at the dosage of 56.0 μg/insect applied topically. In comparison, the introduced alligatorweed flea beetle, *Agasicles hygrophila* Selman and Vogt, is highly susceptible, having an LD_{50} of 0.292 μg/insect (Kreasky et al. 1979). The susceptibilities of these two insects were much closer with methyl parathion [*0,0*-dimethyl *0*-(*p*-nitrophenyl) phosphorothioate], though *A. hygrophila* was again more susceptible, by a factor of 2.6 (LD_{50} 0.025 μg/insect vs. 0.071 μg/insect).

Because aquatic habitats and cropland areas may be subject to potential contamination by heavy metals, the effects of cadmium on the growth of alligatorweed, *Alternanthera philoxeroides* (Mart.) Griseb., and *C. rotundus* and on the feeding and fecundity of *A. hygrophila* and *B. verutana* were studied by Quimby et al. (1979). Cadmium added to nutrient solutions at 1 μg per liter increased the cadmium content of *A. philoxeroides* from 2.6 to 8.7 μg/g and reduced total growth 63%; in *C. rotundus,* cadmium content increased from 2.3 to 6.5 μg/g and reduced growth about 32%. Where *A. hygrophila* proved to be very sensitive to increased cadmium levels, *B. verutana* feeding, fecundity, and longevity were unaffected when larvae were fed on plants with the cadmium concentrations of 6.5 μg/g. In addition, when *B. verutana* larvae were fed on diet containing concentrations of cadmium up to 18.0 μg/g, their feeding and growth were unaffected, as were the subsequent emergence of moths from pupae and the fecundity of the moths.

B. verutana proved to be relatively easy to culture in the laboratory (Sieckert et al.1974 Agricultural Research 1975, Garcia and Frick 1975). Nor have artificial diets proved troublesome. In fact, after several diets were compared by Frick and Wilson (1982), a standard diet produced by the Insect Rearing Section, Southern Field Crop Insect Management Laboratory, Stoneville, Miss., was selected for the large-scale production of *B. verutana* (Frick et al. 1983). This diet was similar to that of King et al. (1979) for rearing larvae of sugarcane borer, *Diatraea saccharalis* (F.). Its composition is given in table 7. In addition, a new type of cage was developed (fig. 6). With its use, oviposition per female increased 21%–35% over other types of cages while at the same time accommodating more pairs of moths per liter (50 pairs/per one 3-liter cage vs. the standard 10 pairs/per one 2-liter cage) (Frick et al. 1983). That plus the other modifications in the cultural methods resulted in the daily production of 90,500 neonate larvae or 2,675 adults per day.

Frick and Wilson (1980) studied the feasibility of utilizing each stage in field releases. The eggs, half-grown larvae, and pupal stages were all rejected because of either difficulty in removal from their substrate, damage increased during removal, lack of efficient methods of concentrating large numbers for release, or the need for rather high relative humidities. From 1972 through 1977, adults or neonate larvae were released in small-scale plots (Frick and Chandler 1978). Because of the ease of harvesting, concentrating, and preparing neonate larvae, a method was developed of mixing them with corncob grits for broadcast with a seed or fertilizer spreader (Frick 1982, Frick et al. 1983). The degree of infestation depended mainly on the density of the host plant—the greater the density, the greater the percentage of larvae infesting the plant (Frick 1982). Adults were aspirated into flasks and tapped out at the point of release (Frick et al. 1983). Considering that at least 50% of the plants must be infested to provide for a signficant reduction of the weedy host plant, effective control was limited. *B. verutana* adults were effective in circles at least 10 m and, unusually, to 20 m in diameter (Frick 1982).

The damage done to *C. rotundus* by the feeding of partially grown larvae (10–18 days old) was enhanced 15%–75% by coating of the larvae with the herbicide glyphosate [*N*-(phosphonomethyl)glycine] (Quimby and Frick 1980). Because larvae 13 or more days old were generally in the fourth instar and had only a limited period of feeding remaining, 10-day-old larvae were selected for additional studies. Frick and Wilson (1978) showed that most of the 10-day-old larvae were in the third instar, with a small percentage already in the fourth; and most had 8–9 days of feeding time remaining.

Coating the larvae caused an additional significant reduction in dry weight of 2-week-old plants, which averaged 25% below the dry weights of those plants fed on by larvae dipped in water (Quimby and Frick 1985). There was no difference in response, whether glyphosate or bentazon [3-isopropyl-1*H*-2, 1, 3-benzothiadiazin-4(3*H*)-one 2,2-dioxide] was used. In contrast, coated larvae reduced dry weights of yellow nutsedge significantly below those of yellow nutsedge attacked by water-dipped larvae in only one-half the studies.

The age of most plants in which releases are to be made is of primary importance to the success of a release. In greenhouse tests, all 2- to 3-week-old plants suffered injury, but 4-week-old plants were only 20% attacked, while 5- to 6-week-old plants were unacceptable to the larvae (Frick and Wilson 1980). Fortunately, in preparation of a seedbed, existing *C. rotundus* plants are destroyed; the tubers, however, are not destroyed, and they sprout new plants of known age. Therefore, beginning about 2 weeks after crop planting, the host plants are in a vigorous growing condition and thus highly susceptible to infestation during the 2–4 weeks of 3–5 weekly releases.

Table 7—*Composition of Nutri-Soy flour/wheat germ diet for rearing larvae of* Bactra verutana[1]

Ingredient	Amount	Source
Nutri-Soy flour (g)	156	Flavorite Lab., Memphis, Tenn., or Archer Daniels Midland, Decatur, Ill.
Wheat germ (g)	133	Nutritional Biochemicals, 26201 Miles Road, Cleveland, Ohio
Wesson salt (g)	38	Same
Sugar (g)	145	Local purchase
Vitamin premix (g)	36	Roche Chemical Division, Nutley, N.J.
Agar (g)	95	Burtonite, Nutley, N.J., or Perney, Inc., Ridgewood, N.J.
Methyl parasept (MPHB) (g)	3.8	Nutritional Biochemicals
Aureomycin (chlortetracycline) (g)	3.8	Animal Services, Forest, Miss.
Sorbic acid (g)	3.8	Nutritional Biochemicals
Mold inhibitor[2] (mL)	15	
Water (mL)	3,535	

[1]Mixing instructions for 3.8-L diet. Premix all dry material and place in blender. Heat water to boiling and add to blender, add mold inhibitor, blend for 4 minutes and pour into cups.
[2]Mix 418 mL of propionic acid with 82 mL of distilled water, mix 43 mL of phosphoric acid with 458 mL of distilled water, then mix the two solutions.

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